

## Temporal Changes in a Tropical Rocky Shore Snail Community

BY

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(1 Text figure)

### INTRODUCTION

MORE SPECIES ARE GENERALLY found in tropical communities than in comparable temperate communities, and rocky shore gastropod assemblages are no exception. On Pacific Ocean rocky shores, the same collecting effort will yield about 2.4 times as many species in Costa Rica as in Oregon (MILLER, 1974). Rocky shores contain the same range of habitats at both latitudes (SPIGHT, 1977). If the average tropical snail uses fewer habitats than a typical temperate one, the tropical species would be more specialized, but overlap among species could be about the same as in temperate waters. Alternatively, tropical snails can utilize the same range of habitats as their temperate counterparts; when this is the case, overlap among species will be much greater than in temperate communities.

To determine whether tropical snails use fewer habitat types than temperate ones do, I collected snails from a number of quadrats at Playas del Cocos, in northwestern Costa Rica during 1970 (SPIGHT, 1976). Each quadrat was characterized by its shore level, substrate, and degree of wave exposure. Using these variables, habitat descriptions were constructed for all species. Most Costa Rican snails use fewer of these habitat types than do typical snails from Washington State (*i. e.*, they are more specialized; SPIGHT, 1977).

Habitat descriptions tell where snails were found, but not how often they were found where they were supposed to be. Tropical snails were found less often on patches of "suitable habitat" (places included in their habitat description) than temperate ones were (SPIGHT, 1977). Many of these "absences" may have been observed because habitat descriptions were not precise enough (*e. g.*, the investigator did not recognize as many habitat types as the

snails do). On the other hand, tropical snails may simply be less predictable than temperate ones.

One can assess predictability by observing how distributions change over time. To assess year-to-year distributional changes, I returned to Playas del Coco in 1971 and resampled 2 quadrats I had examined during 1970. Two questions were asked: 1) are the assemblages at one place similar in successive years, and 2) can year-to-year changes at one place be accounted for by growth of residents and recruitment of juveniles? The discussion will examine the results in terms of habitat selection and other factors causing distributional patterns.

### METHODS

The quadrats are more or less uniform areas of rock reef sufficiently differentiated from the surrounding areas to be readily recognized without artificial markers. The quadrat exposed to moderate wave action (Q-11) is a flat 6 m<sup>2</sup> portion of a highly dissected rock face on the north side of Punta Miga (height, 0.67 m above mean low water [MLLW]). The calm-water quadrat (Q-8) is a 3 m<sup>2</sup> area on the extreme southern portion of Bahía El Coco (height 1.4 m above MLLW). It is protected from oceanic conditions by Punta Miga. Most of the reef near Q-8 is buried by silty sand, but the reef is continuously exposed about 1 m further along the beach (see SPIGHT, 1976, for maps showing quadrat locations and for further sampling details).

On each visit (8 February - 21 March, 1970; 7-14 February, 1971), all gastropods were handpicked from the quadrats. The snails were sorted to species, and all those larger than 6 mm were measured with vernier calipers. Individuals that could be readily identified were re-

Table 1

Comparison of gastropod assemblages found in different years on two rocky-shore quadrats at Playas del Coco, Costa Rica.

Species	Collection of 1970				Collection of 1971			
	N	Shell length (mm)			N	Shell length (mm)		
		Range	Mean	SD		Range	Mean	SD
Quadrat with moderate wave action (Q-11)								
<i>Acanthina brevidentata</i> (Wood, 1828)	47	13-22	16.0	1.52	46	8-20	14.0	3.14
<i>Thais melones</i> (Duclos, 1832)	26	12-37	21.2	5.99	34	13-40	21.0	7.55
<i>Fissurella virescens</i> Sowerby, 1835	33 <sup>1</sup>	21-42	30.1	5.49	87 <sup>2</sup>	—	—	—
<i>Siphonaria maura</i> Sowerby, 1835	5 <sup>3</sup>	10-18	15.0	3.00	14	9-20	14.7	3.24
<i>Fissurella longifissa</i> Sowerby, 1863	51, <sup>3</sup>	19-23	20.8	1.64	+ <sup>2</sup>	—	—	—
<i>Opeatostoma pseudodon</i> (Burrow, 1815)	0	—	—	—	4	9-22	17.0	5.60
<i>Anachis lentiginosa</i> (Hinds, 1844)	0	—	—	—	2	7-8	7.5	—
<i>Thais speciosa</i> (Valenciennes, 1832)	1	9	9.0	—	0	—	—	—
<i>Siphonaria gigas</i> Sowerby, 1825	1 <sup>3</sup>	15	15.0	—	0	—	—	—
<i>Scurria stipulata</i> (Reeve, 1855)	0	—	—	—	1	20	20.0	—
Quadrat in calm-water area (Q-8)								
<i>Acanthina brevidentata</i> (Wood, 1828)	188	6-26	9.9	1.94	252	6-24	17.0	4.16
<i>Anachis costellata</i> (Broderip and Sowerby, 1829)	246	5-18	13.6	2.71	105	6-19	13.4	3.71
<i>Anachis lentiginosa</i> (Hinds, 1844)	69 <sup>3</sup>	3-6	—	—	127	—	—	—
<i>Anachis rugulosa</i> (Sowerby, 1844)	133 <sup>3</sup>	3-6	—	—	134	—	—	—
<i>Nerita funiculata</i> Menke, 1851	92	3-13	7.5	2.20	45	3-12	8.4	2.24
<i>Thais biserialis</i> (Blainville, 1832)	53	4-24	12.3	4.87	76	5-38	13.7	7.77
<i>Fossarius</i> sp.	12 <sup>3</sup>	3-5	—	—	14	—	—	—
<i>Anachis pygmaea</i> (Sowerby, 1832)	6	6	—	—	6	—	—	—
<i>Notoacmea biradiata</i> (Reeve, 1855)	8 <sup>3</sup>	6-11	8.9	1.73	0	—	—	—
<i>Purpura pansa</i> Gould, 1853	1	32	32.0	—	0	—	—	—

<sup>1</sup>Collected from only 1 m × 2 m portion of quadrat; all others are numbers for entire 2 m × 3 m quadrat (Moderate wave action) or entire 1.5 m × 2 m quadrat (Calm-water).

<sup>2</sup>Fissurellids were counted (on entire quadrat) but not measured in 1971, and the species were not separated; both species were present.

<sup>3</sup>All specimens collected in 1970 were removed permanently from the quadrat; for other species all but a few voucher specimens were returned to the quadrat within a few days after collection.

turned to the quadrat within 24 hours; other individuals were preserved for later study.

Some Q-11 snails were tagged to obtain growth rates. On 8 February 1970, 66 *Thais melones* (Duclos, 1832), 30 *Acanthina brevidentata* (Wood, 1828) and 10 *Opeastoma pseudodon* (Burrow, 1815) were given individually numbered tags and returned to Q-11. When the complete collection was made (8 March 1970), 23 of these snails were recaptured, and on 21 March, 11 additional tagged snails were captured. No tagged snails were found in 1971.

To evaluate the growth data, the observed increments of shell length were regressed on initial size. Of the 3 regressions, only that for *Acanthina* over the 8 February-8 March interval was significant ( $F_{1,8}=4.15$ ;  $0.10 > P > 0.05$ ). Since growth was poorly correlated with size, the data are presented here as unweighted averages.

## RESULTS

The collections made in 1971 are much more similar to those taken from the same quadrats in 1970 (Table 1) than to collections from other quadrats (SPIGHT, 1976). For most species, both density and mean shell length were similar in 1970 and 1971. Furthermore, most of the individuals kept for vouchers after the 1970 collection had been replaced by others of the same species by 1971.

Species lists for the 2 years are not identical. Of the 18 species collected, 4 were found only in 1970, and 3 were found only in 1971 (Table 1). However, of these 7 species only *Notoacmea biradiata* was represented by as many as 8 individuals (1970; these were preserved).

Densities and size distributions also changed between years (Figure 1). Along with limited growth data, these size distributions reveal the underlying processes that

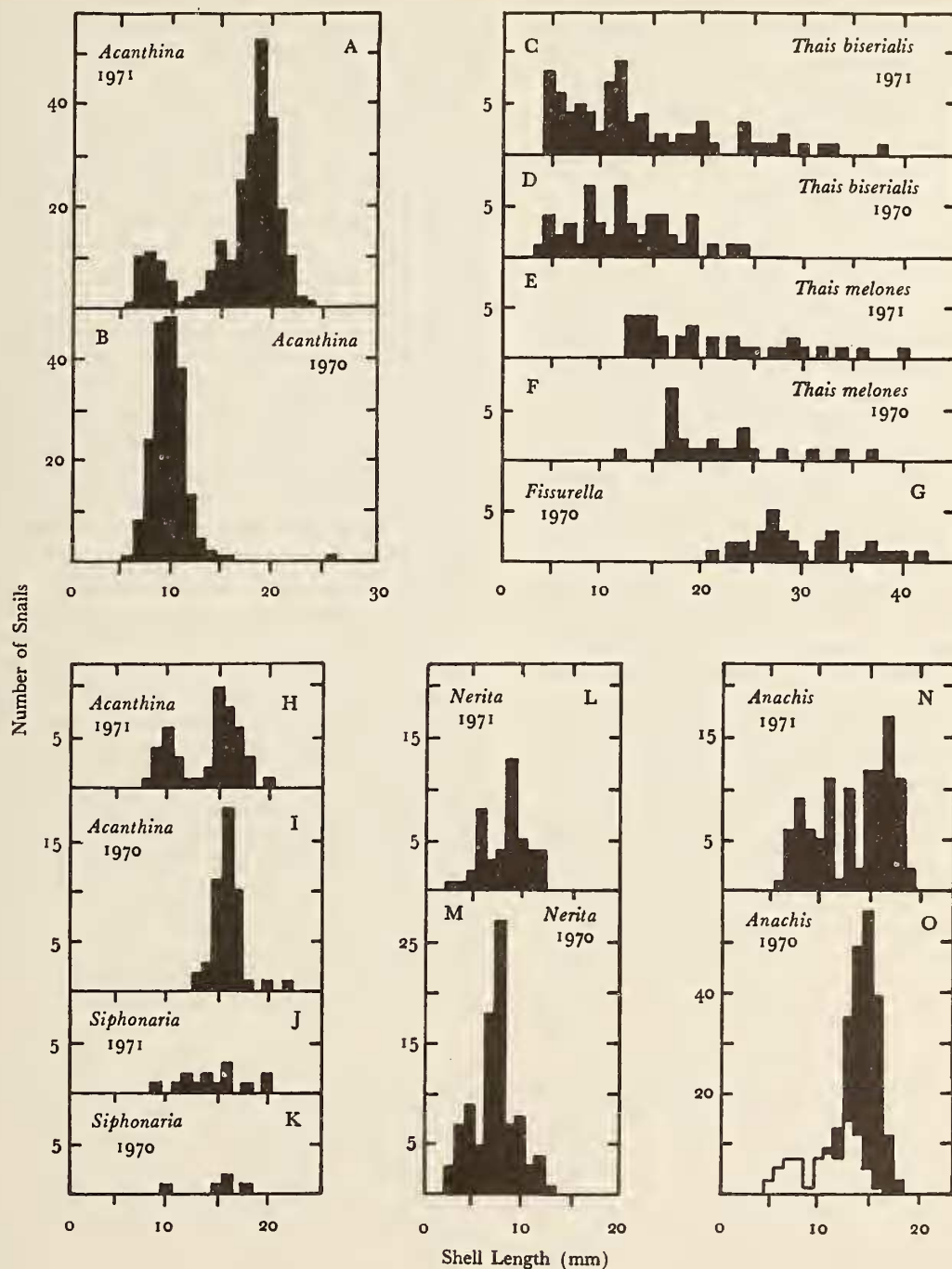


Figure 1

Sizes of snails collected from Q-8 and Q-11 during 1970 and 1971. *Acanthina brevidentata* (A, B), *Thais biserialis* (C, D), *Nerita funiculata* (L, M), and *Anachis costellata* (N, O) were collected from Q-11, while *Thais melones* (E, F), *Fissurella virescens* (G),

*Acanthina brevidentata* (H, I), and *Siphonaria maura* (J, K), were collected from Q-11. Note that the vertical scales for A, B, and O are twice those for all other figures. The white columns on O refer to snails with thin lips, and the dark columns to snails with thick lips.



maintain the composition of these gastropod assemblages. The data will be reviewed for each of the major species in turn.

*Acanthina brevidentata* — The size distributions have definite peaks (Figure 1-A, B, H, I), and these probably correspond to year classes. The first peak is at about 10 mm, which is at the lower end of the yearling size range for typical temperate *Thais* (*T. emarginata* (Deshayes, 1839), *T. lamellosa* (Gmelin, 1791) and *T. lapillus* (Linnaeus, 1758) (SPIGHT, 1975). The second peaks are at about 16 mm and 19 mm, the latter typical for second-year *T. emarginata* and *T. lapillus* (SPIGHT, 1972; FEARE, 1970a). However, 8 - 10 mm annual increments would require more rapid growth than that actually measured during the February-March period of 1970 (Table 2).

Known spawning times are consistent with these age assignments. *Acanthina* deposited eggs on Q-8 during February, 1971, and elsewhere during March, 1970. If most snails spawn during February and March, then the smaller size peak (Figure 1) would represent snails almost exactly 1 year old. However, temperate muricids that attain only 20 - 25 mm as adults spawn more than once (*Thais lapillus*, FEARE, 1970b) and frequently repeatedly throughout the year (*T. emarginata*, HOUSTON, 1971; *Eupleura caudata* (Say, 1822), MACKENZIE, 1961). *Acanthina* may also have a long spawning season.

The size distributions (Figure 1) indicate that many more recruits settled at some times and places than others. The size distribution for each quadrat is unimodal in one collection and bimodal in the other. In 1970, the Q-8 population consisted entirely of yearlings, and the Q-11 population entirely of adults. Yearlings

were present on both quadrats in 1971, but fewer were found on Q-8 than had been found in 1970. Thus, during 1969 many snails recruited to Q-8, while only a few recruited to nearby Q-11.

The estimated annual growth performances and the observed dry-season growth rates are lower than typical temperate ones. Snails grow slowly when food is sparse (SPIGHT, 1972) and food supplies appeared to be sparse at Playas del Coco. The major prey of *Acanthina* is *Chthamalus* (PAINE, 1966). The most common species at Playas del Coco, *C. panamensis*, is small and was sparse on both visits. Both barnacles and mussels were more abundant on Q-8 than on Q-11, and, appropriately, snails grew faster and reached larger sizes on Q-8.

The Q-8 is a sandy area, and sand levels shifted during the observation period. At times the entire Q-8 area is probably submerged by the sand. The *Acanthina brevidentata* on this quadrat were unusually numerous, and many more juveniles were found here than elsewhere. The size distributions may indicate recolonization after a recent burial.

*Thais melones* — The size distributions and growth data indicate growth rates similar to those of *Acanthina*. Most snails found were 15 - 25 mm (Figure 1-E, F) and these are assumed to be second year juveniles. Since the second-year snails of 1971 are not represented as first-year snails in 1970, the actual annual growth performances are not clear. If snails settled after the 1970 visit, they must have reached 15 - 25 mm in 10 months or less. However, the tagged snails grew much more slowly. Alternatively, the snails settled before the 1970 visit and I failed to observe them. Since the crevices on the quadrat

Table 2

Net growth by three Costa Rican snails during the 1970 dry season.

Species	N	Size Range (mm)	Net Size Increase (mm)		SD	r
			Maximum	Mean		
8 February to 8 March						
<i>Thais melones</i>	13	12-36	1.0	0.49	0.29	0.094
<i>Acanthina brevidentata</i>	10	11-22	1.6	0.21	0.50	-0.584
8 February to 21 March						
<i>Thais melones</i>	9 <sup>4</sup>	15-29	2.6	0.80	0.84	-0.240
<i>Acanthina brevidentata</i>	2 <sup>5</sup>	15-16	0.5	0.45	—	—
<i>Opeatostoma pseudodon</i>	1	17	2.6	2.6	—	—

r, correlation between initial size and net size increase

<sup>4</sup>includes one of the snails recaptured 8 March

<sup>5</sup>neither snail recaptured 8 March

could provide hiding places for most snails 4 - 6 mm long, the 15 - 25 mm snails of 1971 could have settled as early as October or November, 1969. Assuming that fall is the normal settlement period, the year classes of 1968 and 1969 were about equally large, and the 1968 snails grew slightly faster than the 1969 ones.

The *Thais melones* size range is similar to that of *T. lamellosa* (SPIGHT, 1974), and therefore a similar mature size of 25 - 35 mm can be expected for Playas del Coco snails.

*Thais biserialis* — The size distributions do not have discrete peaks (Figure 1-C, D), and therefore growth rates cannot be derived. Most snails were 4 - 20 mm, and these were probably first and second year juveniles. The continuous size distribution suggests continuous recruitment, in contrast to *Acanthina*. The size range should correspond to an adult size greater than 25 mm (which is unusually large for a species that breeds throughout the year; SPIGHT *et al.*, 1974). No adults were present in 1970, and only a few were found in 1971. If the 1971 adults were among the juveniles collected in 1970, then each must have grown about 10 mm during the year. The dense population of juveniles may indicate a recent colonization of Q-8.

*Anachis costellata* — Shell morphology may indicate maturity, allowing snails to be aged. In 1970, the smaller snails had thin lips and rounded shoulders, while the larger ones had thick lips and square shoulders. If a thickened lip indicates maturity, then most snails mature at about 13 mm (12 mm is the largest size at which more than half of the 1970 snails had thin lips (Figure 1-O); morphologies were not noted in 1971). The size distribution was unimodal in 1970 (Figure 1-O) and bimodal in 1971 (Figure 1-N). If the 2 modes represent year classes, then the snails grew about 10 mm during their second year. Many adults and few juveniles were found in 1970, while the same collection (from Q-8) yielded many juvenile and few adult muricids.

*Nerita funiculata* — Size distributions for 1970 and 1971 (Figure 1-L, M) are more similar than those for any of the other Q-8 species. Both have the same mode at 7 - 9 mm, suggesting that this species is an annual. On Barbados, 3 *Nerita* species all reach 10 - 13 mm in their first year (HUGHES, 1971b; all are mature at 14 mm or more), and similar growth rates might be expected in Costa Rica.

*Fissurella virescens* — These limpets (measured only in 1970) have a unimodal size distribution (Figure 1-G). No 0 - 20 mm *Fissurella* were found. Either snails did not settle during 1969 or those that did grew rapidly. *Fissurella barbadensis* Gmelin, 1791 reaches about 26 mm dur-

ing its first year and generally not more than 30 mm (HUGHES, 1971a), while *F. virescens* frequently reaches 40 mm (Figure 1-G). If *F. virescens* and *F. barbadensis* both grow at the same rate during the first year, then the 20 - 30 mm limpets from Q-11 would be yearlings.

## DISCUSSION

The answer to both questions posed in the introduction is "yes." The assemblage of snails found on each quadrat in 1971 was very similar to that found on the same quadrat in 1970 — that is, much more similar than to the assemblage on any other quadrat at the same time. Furthermore, each species population was similar to the previous year's because juveniles grew and recruits settled and established themselves. The individuals I removed in 1970 were replaced by recruits prior to the 1971 collections. If these 2 quadrats are typical, then the marked faunal differences among quadrats (SPIGHT, 1977) are a persistent feature of this tropical site rather than an ephemeral feature which arises because snails are habitat generalists and are wandering from habitat to habitat.

If distributions are persistent, do they reflect habitat selection, or could they arise through less predictable processes? Habitat selection ultimately reflects factors which affect the success of a species in different habitats. Both physical and biological factors affect success, and both lead to orderly and patchy distributions in temperate communities. Each shore level has a different regime of physical stresses. Species that tolerate the dehydration and temperature stresses of one level are often unable to tolerate the greater stresses found at higher levels and may be rapidly exterminated by predators at lower shore levels (CONNELL, 1972). As a result, most species have well-prescribed vertical (shore level) ranges, and these are the basis for universal schemes of shore zonation (STEPHENSON & STEPHENSON, 1972). Similar physical regimes in the more diverse tropical community could lead to even finer vertical division of the shore habitat.

For temperate rocky shore species, physical and biotic factors also lead to patchy distributions. Recruits from many intertidal species are much more abundant in some years than others (COE, 1956; LOOSANOFF, 1964; SPIGHT, 1975), food supplies are unpredictable (SPIGHT, 1972), encounters with predators are both irregular and locally devastating (PAINE, 1974), and physical stresses are often near the tolerance limits of individuals (DAVIES, 1969; FOSTER, 1971). Within a shore level, these physical and biological stresses result in a continuing race between local extinction and recolonization (SPIGHT, 1974). Colonists



establish themselves as patches become available on the shore, and for the most part, the patches bear little relationship to the nature of the physical habitat (CONNELL, 1970; DAYTON, 1971; PAINE, 1974). With more species in the tropical community, there should be more kinds of biotic interactions, and these could, in turn, lead to more unpredictable distributions.

The changes that did take place between years (Figure 1) do imply that these same physical and biotic processes are important at Playas del Coco. Recruits from most species were much more numerous during one year than the other. *Acanthina brevidentata* was abundant on both quadrats and recruits of this species were most abundant on the 2 quadrats at different times. Thus, recruitment appears to be as unpredictable as it is in temperate waters. Tropical snails grew slowly by both measures used (tag returns and analysis of size distributions). Snails usually grow slowly because food is scarce (SPIGHT, 1972), and even a predictably sparse food supply presents a major stress. The snail sizes on Q-8 suggest recolonization after a recent burial in sand, and thus unpredictability of the physical environment. Also, more kinds of predators eat snails and together these predators are more numerous at Playas del Coco than at most temperate sites (personal observations). Activities of predators are a major cause of unpredictability in temperate waters. Appropriately, amid this array of physical and biotic stresses, the snail populations had not attained stable age distributions and showed no other evidence that the tropical rocky shore environment is more predictable for them than the temperate one.

The distributions observed at Playas del Coco were persistent, but this does not necessarily indicate that they arose by habitat selection. Patchy distributions will arise and persist despite a uniform landscape if colonizers settle patchily and subsequent species interactions maintain the patches (LEVIN, 1974). For example, unique assemblages developed and persisted in each of the artificial oak logs placed by FAGER (1968). The assemblages were best described as results of random colonization sequences to otherwise uniform habitats. Patches of some sedentary intertidal species persist for at least 6 years (PAINE, 1974). Although most species found on Q-8 and Q-11 were found on both visits, the snails may have colonized these sites fortuitously; had other species arrived earlier, quite different assemblages could have developed and persisted. Therefore the present data provide no information about habitat selection and its potential role in the function of diverse tropical communities.

Persistent distributional patterns are amenable to experimental analysis, and experiments should clarify the

role of habitat selection in tropical shore communities. Transplant experiments can be united with habitat modifications and selective removals to reveal factors influencing larval settlement and adult migrations. Such experiments will add a great deal to our now meager understanding of how tropical gastropods use shore habitats.

## SUMMARY

Censuses of rocky shore gastropods were taken from 2 quadrats in northwest Costa Rica in 1970 and repeated in 1971. For most species, densities and average shell lengths did not change significantly. Recruitment varied in both time and space. Growth rates of thaisids were low relative to those of temperate species, in keeping with apparent scarcity of food. Distributional patterns may reflect habitat selection by the snails, but they may also be consequences of random colonizations and subsequent biotic interactions.

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